The ultrastructure of the lachrymal 'salt' gland and the Harderian gland in the euryhaline *Malaclemys* and some closely related stenohaline emydines

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The ultrastructure of the Harderian gland from the euryhaline species *Malaclemys terrapin* is nearly identical with that of the Harderian gland from several freshwater and stenohaline emydines. The abundant rough-surfaced endoplasmic reticulum, and the prominence of the secretory droplets throughout most of the cytoplasm, indicate that this gland is primarily involved in the secretion of organic materials, and has no role related to the salinity of the environment in which the animals are kept. However, the ultrastructure of the lachrymal gland in *Malaclemys* differs markedly from that of the remaining emydines studied. In the freshwater emydines the lachrymal gland appears to be involved in the secretion of organic material; the tubules contain both mucous and serous cells. In the lachrymal gland from *Malaclemys* secretory droplets, Golgi apparatus, and endoplasmic reticulum were insignificant features, while mitochondria, glycogen, and microvilli on the serosal surfaces of the cells were very prominent. These and other features cause a strong resemblance between the lachrymal gland in *Malaclemys* and other tissues noted for active transport. The above morphological evidence suggests that if either of the orbital glands is involved in osmoregulation the most probable choice is the lachrymal gland.

Introduction

Schmidt-Nielsen and Fänge (1958) precipitated renewed interest in reptilian orbital glands with their discovery of extrarenal excretion in the marine chelonians and the euryhaline *Malaclemys*. In that paper Schmidt-Nielsen and Fänge reported the collection of hypertonic solutions of sodium chloride from the orbital region in *Malaclemys*. The source of the secretion was uncertain, and no details of the collection methods used or of sodium concentration in the collected fluid were given. Dunson and Taub (1967) reported the collection of hypertonic solutions of sodium chloride from what they referred to as the Harderian gland in *Malaclemys*. The paper by Dunson and Taub (1967) appeared after I had begun a study on the orbital region of a variety of emydine turtles, including *Malaclemys*. That work, which was summarized earlier (Cowan 1967 and 1969), showed that all emydines possessed two orbital glands. A basis for nomenclature was put forward (Cowan 1969 and 1970) and the two glands were homologized with the Harderian and lachrymal glands of various reptilian and avian species. In the earlier work I found that the Harderian gland was of constant size, and the histological structure and histochemistry were identical in all the emydines studied, including *Malaclemys* and euryhaline species. The lachrymal gland in *Malaclemys* was much larger and had some contrasting histological and histochemical characteristics when compared to the lachrymal glands from all the freshwater species. This suggested that the lachrymal gland in *Malaclemys* was involved in some function related to salinity. Changes in the histochemistry of lachrymal glands from *Malaclemys* moved from fresh water to seawater supported that idea (Cowan 1969). However, some of the gross anatomical findings described in the same paper (Cowan 1969) aroused some doubt about the validity of the methods used by Schmidt-Nielsen and Fänge (1958) and Dunson and Taub (personal communication). However, if either orbital gland was involved in osmoregulation my earlier studies indicated that the most likely choice would be the lachrymal gland.

I decided to investigate the ultrastructure of the orbital glands from the euryhaline *Malaclemys*, and some closely related freshwater species from the genera *Graptemys*, *Pseudemys*, and *Chrysemys*, with the following objectives. The first objective was to see if the uniformity of the Harderian gland, as seen in the light microscope, was also apparent at the ultrastructural level. Secondly I wished to confirm, with the help of the electron microscope, that the lachrymal gland of several stenohaline species was similar and probably involved in the secretion of organic material. Finally I

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wished to confirm the initial impression gained from light microscopy that the structure of the lachrymal gland of the euryhaline *Malaclemys* was different from that of stenohaline species, and further that the lachrymal gland from *Malaclemys* was apparently not involved in secretion of organic material. The results will show this to be the case, and in fact the ultrastructure of the lachrymal gland in *Malaclemys* has a marked resemblance to many organs involved primarily in the secretion of inorganic electrolytes.

**Materials and Methods**

*Malaclemys terrapin* were obtained from Mr. Miles Hancock of Chincoteague, Virginia, in a field trip to that community, and indirectly from the same source through a retail outlet in Toronto. The *Malaclemys* from Chesapeake Bay represent an intergrade between two subspecies *Malaclemys t. terrapin* and *Malaclemys t. centrata*. A third subspecies, *Malaclemys t. macrospilota*, from the Gulf of Mexico was obtained from a commercial aquarium supplier, as were specimens of *Graptomys barbouri*, *Chrysemys picta marginata*, *Graptomys pseudogeographica pseudogeographica*, and *Pseudemys scripta elegans*.

All specimens were kept in glass or plastic tanks at ambient room temperature. This ranged from 18 to 23 degrees Centigrade. The animals were fed shrimp, fish, and occasionally lettuce, at 3-day intervals.

The specimens from the genera *Graptomys*, *Pseudemys*, and *Chrysemys* were kept in ‘fresh water.’ This was made up as 1 kg of dechlorinated tap water at 22°C containing 1.7 mmole of sodium chloride and 0.87 mmole of calcium chloride. These amounts compare well with those contained in fresh water as reported by Potts and Parry (1964). *Malaclemys* were kept in artificial seawater made from a preparation called Instant Ocean (Aquarium Systems Inc., Ohio). Full strength seawater (100% seawater) made from this preparation has a specific gravity of 1.025 at 25°C.

Fixation for electron microscopy, in most cases involved immersion fixation of small cubes, about 1 mm on each side, which had been rapidly dissected from decapitated animals. Anesthetics were avoided as some of these have been shown to affect salt gland function in some species (Schmidt-Nielsen and Fänge 1958). Fixation after anesthesia was also shown to have an effect on ultrastructure in the present work with turtles (Cowan, unpublished). The fixatives used were 1.0% osmium tetroxide, 1.0%, 2.5%, and 5.0% glutaraldehyde, and 10% formaldehyde-calcium. These fixatives were used as single fixatives, or with osmium tetroxide postfixation after glutaraldehyde or formaldehyde prefixation. Sorenson’s phosphate buffer, pH 7.36, with an osmolality of 298 mosmols was the buffer more commonly used; however, a series of modified Tyrode’s solutions, with molarities ranging from 305 mosmols to 463 mosmols, was also used. This buffer series as devised by Maunsbach (1966) contains sodium chloride in amounts ranging from 0.4 to 1.0 g/100 cc, in addition to the substituents normally used in Tyrode’s solution. Cadaveric buffer (0.067 or 0.135 M) was also used to buffer glutaraldehyde.

After immersion fixation the tissue was dehydrated in graded ethanols, cleared in propylene oxide, and embedded in Epon 812-Araldite. Sections were cut on a Porter-Blum MT-2 ultramicrotome and collected over acetone diluted 1:19 with distilled water. Initially the examination of the sections was with unstained material; however, subsequent work used sections stained in uranyl acetate or lead citrate solutions (Reynolds 1963).

**Observations**

The similarity of the Harderian gland in the various emydines, as seen in the light microscope (Cowan 1969), is confirmed at the ultrastructural level for all species examined. One description can apply to all the examined material. The cells are columnar, 20 micra high by 8 micra wide, with apices bordering on a lumen of variable diameter. The apical three-fourths of the cell is filled with large secretory droplets. (This is more apparent in a larger population of cells as seen in light microscopy (Fig. 1).) These droplets are up to 2 micra in diameter and are surrounded by a single unit membrane. Free ribosomes, saccules of smooth endoplasmic reticulum, which are arranged in parallel stacks, and a complex array of rough-surfaced endoplasmic reticulum are situated between the secretory droplets and the nucleus (Fig. 2). This area corresponds to the region which stains metachromatically with toluidine blue at pH 4.5 (Cowan 1969).

The epithelium rests on a straight basement membrane, and there are no invaginations or complicated processes increasing the basal surface area. Laterally the cell membranes are also straight (Fig. 2) and are closely apposed in all species and despite variations in fixative toxicity or in the media in which the animals were kept. The space between the cells in the Harderian gland was always held between 200 and 300 Ångstrom units by a junctional complex apically and desmosomes along the lateral borders.

The connective tissue stroma is quite simple. Myo-epithelial cells could not be identified. Few nerves were found, and those that were located seemed associated with the blood vessels. There were no nerve endings closer to the tubular epithelium than to the capillary endothelium. The vascularity of the Harderian gland is low.
(Fig. 1), with only an occasional vessel or endothelial cell being seen in a given electron microscopic section. This differs markedly from the highly vascular stroma of the lacrimal gland in both stenohaline and euryhaline species.

The ultrastructure of the lacrimal glands from all the stenohaline species is similar, as is true of the light microscopy and histochemistry, and apparently indicates that these cells are involved in the secretion of organic materials (see also Cowan 1969). What appear to be two types of cells with light microscopy represent two series of distinct cell lines. The most numerous contain large and moderately electron-dense secretory droplets which pack the apical two-thirds of the cytoplasm. These cells apparently correspond to the PAS-negative cells seen in the light microscope (Cowan 1969). The second type of secretory cell is less numerous and contains large secretory droplets which are electron transparent (Fig. 3). These cells correspond to the PAS-positive cells seen in the light microscope.

The two types of cells have most features in common. The apical cell border of both types is covered with short microvilli, and the apical end bulges into the lumen, reducing its diameter to about 2 micra. The entire apical half of the cells of both types is filled with secretion. The lateral borders are straight, without complicated interdigitations (Fig. 3), and held closely opposed by desmosomes along their length. A junctional complex binds together the apical ends of the adjoining cells. Both cells lie on a prominent basement membrane.

The major differences between the two types of cells other than the density of the secretory droplets are the cell sizes and the endoplasmic reticulum. The cells with electron-dense secretions are much larger as well as being more numerous. In these large cells there is a very complex, rough-surfaced endoplasmic reticulum basal to the secretion. Lysosomes and scattered mitochondria lie between the cisternae. The latter are small and do not contain dense granules. A small Golgi apparatus is located near the nucleus. The smaller type of cell, which corresponds to the PAS-positive cell, is shown in Fig. 3. It shows the same features as the larger cell with the exceptions that the secretory droplets are electron transparent, the Golgi apparatus is much more extensive, and the rough-surfaced endoplasmic reticulum is somewhat less complex (Fig. 3).

The tubules in the lacrimal glands of the stenohaline species are well supplied with blood vessels. The nerves are associated only with the adventitia of the vascular elements as far as can be ascertained. These endings contain either large vesicles, 600 Ångstrom units in diameter, or smaller vesicles of 200 Ångstrom units without internal structure. As will be reported elsewhere, these nerve endings were stained by acetylcholinesterase methods for acetylcholinesterase. I saw no nerve endings in close proximity to parenchymal cells or penetrating through the basement membrane of the tubular epithelium in the stenohaline lacrimal gland.

The lacrimal gland in the euryhaline *Malaclemys terrapin* stands in striking contrast to that of the stenohaline species. The cells are about the same size but the resemblance stops there. Apically the cell membrane is smooth, but with a few small blebs, and borders a lumen of variable but relatively large diameter (Figs. 4 and 5). Laterally the cell membranes of neighboring cells are bound together at their apices by junctional complexes (Fig. 4), but basal to these complexes the lateral cell membranes bear long microvilli (Figs. 4, 5, and 6). In some cases these microvilli interdigitate with microvilli of neighboring cells, and in others the microvilli are reflected against the side of the cell from which they originate (Fig. 4). The microvilli are up to 1 micron long and contain a dense central core, which may consist of fine fibrils. The membrane covering the microvilli is a unit membrane identical with that covering the rest of the cell surface. Neighboring cells are infrequently bonded together along their lateral membranes by desmosomes between adjacent microvilli. These desmosomes are rare, and thus the size of the intercellular space may vary under a variety of conditions (Figs. 5 and 6).

The basal cell membrane of the tubular epithelium is also complex. The basal ends of the cells bear many processes which are embedded into connective tissue of the stroma. These major processes, which superficially resemble renal podocytes, also bear microvilli. In many cases the cell appears to contact the underlying connective tissue only through a number of these
thin processes (Fig. 6). This appearance is probably due to the section having passed through the periphery of the cell. Centrally the contact of the cell with the basement membrane is less fragmentary. The type of architecture just described results in a direct communication of the intercellular space with the basement membrane (Fig. 6), without intervening cell membranes. In summary the main features with reference to the periphery of the cell are the great area of the cell surface basally and laterally compared to that present apically.

The most prominent feature of the cytoplasm of the cells in the lachrymal gland of *Malaclemys* is the number of mitochondria (Figs. 5, 6, and 7). These mitochondria reach 8 micra long and are usually orientated parallel to the lateral surface of the cell. The intercristal matrix of the mitochondria is dense and contains large very electron-dense granules. These granules are equally abundant in the mitochondria from animals maintained in fresh water or in seawater.

Another prominent feature of the parenchymal cells is the Golgi apparatus (Fig. 7). This organelle may be very extensive and its extent appears to bear no relation to the amount of secretion present apically. The stacked cisternae lie parallel to the lateral cell membranes. Condensing vacuoles or newly formed secretory vacuoles are found between the Golgi apparatus and the nucleus. Lysosomes most often occur in the vicinity of the Golgi apparatus, interspersed with secretory vacuoles (Fig. 7).

Despite the large Golgi apparatus found in some cells, there is little or no smooth-surfaced or rough-surfaced endoplasmic reticulum and usually very little secretion (Figs. 4 and 5). Scattered segments of rough-surfaced endoplasmic reticulum are found throughout the cytoplasm as sparsely distributed single profiles, up to 2 micra long. The amount of secretion is variable, but never abundant as was the case with the stenohaline lachrymal gland.

The only other features of the cytoplasm in the tubular cells of the lachrymal gland in *Malaclemys* are glycogen (Fig. 7), lysosomes (Figs. 5 and 7), and occasional multivesicular bodies. Some of the features described above vary in morphology after different fixative regimens, and depending on whether the animal was kept in fresh or distilled water. These effects will be described elsewhere (Cowan, unpublished).

Two other types of cell are found in the tubules of the lachrymal gland from *Malaclemys*, the basal cells and the cells with the morphology but not the staining of goblet cells. The basal cells (Figs. 6 and 8) are possibly generative cells and will be discussed elsewhere (Cowan, unpublished). The goblet-like cells are of unknown function, and are very few in number.

The lachrymal gland in *Malaclemys* is highly vascular (Fig. 9), and many nerves are embedded in the connective tissue underlying the tubules. In addition nerves penetrate the basement membrane, so that nerve endings are found in the intercellular space between tubular cells (Fig. 10). These endings contain large vesicles with very electron-dense granules (Fig. 10). These will be described more fully in another paper, but electron histochemistry indicates that these vesicles contain catecholamines. In addition to the nerve processes, nerve endings, and vascular elements, the subepithelial connective tissue contains many pigment cells (Fig. 9). It was cells of this type which interfered with the interpretation of autoradiographs; notice especially how the small pigment granules cluster next to the nucleus confounding autoradiography at the light microscopic level.

**Discussion**

The comparative ultrastructural study of the Harderian gland in the stenohaline genera *Pseudemys*, *Graptemys*, and *Chrysemys*, and in the euryhaline *Malaclemys*, indicates that it is not the source of hypertonic sodium chloride solutions collected by earlier authors (Schmidt-Nielsen and Fänge 1958; Dunson and Taub 1967) from *Malaclemys*. The impression obtained from a study of the histology of this gland in various emydines (Cowan 1969) is supported by a study of ultrastructure. This impression is that the Harderian gland in all the emydines studied has a similar function in the secretion of organic material which probably contains protein. The abundant secretory droplets, the extensive rough-surfaced endoplasmic reticulum, the apocrine nature of the secretory process, and the lack of surface specialization (Abel and Ellis 1966) all tend to indicate that the Harderian gland is not
involved primarily in the secretion of electrolytes, despite early statements to the contrary (Dunson and Taub 1967). There is some support for this also in the fact that the Harderian gland was identical in the euryhaline and stenohaline species. Further the Harderian gland from *Malaclemys* kept in seawater was identical with the gland taken from *Malaclemys* kept in fresh water.

The remaining orbital gland in the emydines studied is the lacrimal gland. Homologies of this and the Harderian gland with cranial glands in a variety of other orders will be considered in another paper (Cowan, unpublished). The lacrimal gland in emydines is considered to be homologous to the lacrimal gland in Chelonia. In Chelonia it appears well established that the lacrimal gland is involved in salt secretion, a conclusion based on both morphological (Abel and Ellis 1966) and physiological (Schmidt-Nielsen and Fänge 1958) evidence. The present paper provides morphological evidence that the lacrimal gland in *Malaclemys* might also be involved in salt excretion.

The first line of evidence relates to the fact that the lacrimal gland in all the stenohaline emydines studied is similar and appears to be involved in the secretion of organic material, while such a function is not apparent in the lacrimal gland from the euryhaline *Malaclemys*. In the stenohaline species the ultrastructure was consistent with the conclusion presented earlier (Cowan 1969) that the lacrimal gland in stenohaline emydines is a mucouserous gland.

In that earlier paper it was difficult to assess the function of the lacrimal gland in the euryhaline *Malaclemys*, although there was some indication that this function was related to the salinity of the environment. This conclusion was based on changes in weight, lack of secretory droplets, and an increase in sulfate polyanion staining within and surrounding the cells from the lacrimal glands in animals kept in seawater. The electron micrographs confirm the lack of structures normally found in mucous or serous gland cells. Although a Golgi apparatus is sometimes prominent, endoplasmic reticulum profiles and secretory droplets are very limited. An interesting lack of correlation was found between the strength of sulfate staining and the amount of secretion present in the cells from lacrimal glands of animals kept in seawater.

The lacrimal gland in *Malaclemys* resembles much more closely a variety of organs involved in osmoregulation. The increased area of the basal and lateral surfaces indicates a development to facilitate absorption through the serosal surfaces. This specialization is associated with a large number of mitochondria orientated parallel to the lateral cell membrane. In these and other features the lacrimal gland from *Malaclemys* closely resembles the nasal salt glands in birds (Doyle 1960; Komnick 1963a and b; Ernst and Ellis 1969), the rectal gland of elasmobranchs (Doyle 1962; van den Bergh 1968); and some segments of the reptilian kidney (Robert and Schmidt-Nielsen 1966; Schmidt-Nielsen and Davis 1968). In the latter case the tubule cells of the reptilian kidney are almost identical with this cell of the lacrimal gland in *Malaclemys*. There is also a strong resemblance to segments of the human nephron (Rhodin 1958) and to the striated duct of the human salivary glands (Scott and Pease 1959). In the kidney and the salivary glands the increase in cell surface area basally is due to invaginations in the basal membranes, which are closely associated to elongate mitochondria. The lateral cell membranes in these two organs are relatively straight and held closely apposed by numerous desmosomes. This structure may be related to the transport of electrolytes from the mucosal to serosal surfaces (Diamond and Bossert 1967) although not necessarily so. In both reptilian and avian salt glands transport is in the opposite direction. In these organs there is an increase in serosal surface area by means of projections on the basal and lateral surfaces of the cells. These microvilli border on a lateral intercellular space, which is of variable dimensions (Cowan, unpublished). These variations may be related to those described by Diamond and Bossert (1967, 1968) in their treatment of standing gradient osmotic flow.

In summary the ultrastructure of the lacrimal gland in *Malaclemys*, alone of all the emydines examined, indicates the possibility that it might be involved in osmoregulation or in some function related to the salinity of the environment. I acknowledge the relatively tenuous nature of evidence derived from static morphological studies. For example, the thin loop of Henle, thought to be involved in active transport
on the basis of physiological evidence, shows none of the ultrastructural characteristics commonly supposed to be associated with increased energy metabolism and active transport. Conversely salivary glands show many of the characteristics found in organs specialized for active transport, yet secrete isotonically (Young and Schogel 1966). However, physiological study with detailed anatomical knowledge might be equally susceptible to error (see Cowan 1969), and the present work indicates that of the two orbital glands present in the emydines, the lachrymal gland is most likely the source of the secretion collected by earlier authors (Schmidt-Nielsen and Fange 1958; Dunson and Taub 1967). Using this information, further physiological experimentation can be undertaken (Cowan, unpublished). Further study of this gland would seem especially constructive because unlike the fluid secreted by the avian salt gland (Holmes and McBean 1964) the fluid secreted by reptilian salt glands has a toxicity that appears related to the osmotic stress (Dunson 1970). Thus correlative ultrastructural studies can be made with gland secreting fluid with toxicities varying over a wide range.

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**Explanation of Figures**

**Fig. 1.** Harderian gland of Malaclemys terrapin kept in sea water for 3 months. This figure gives a survey view of the granules which occupy the apical three-fourths of the cells in that gland. The basal nucleus is surrounded by an area which stains metachromatically with toluidine blue at pH 4.4. Epon–araldite thin section stained with toluidine blue. 750 X. **Fig. 2.** Harderian gland from Malaclemys as in Fig. 1 showing extensive rough-surfaced endoplasmic reticulum. The secretory droplets closest to the base of the cell (to the left of the figure) have a moderate electron density (S1). Towards the apex the secretory droplets become more
electron-lucent (S₂) and (S₃). The secretory droplets are bounded by a single unit membrane (MS) and there is some fusion of the material between adjacent droplets (arrows). The lateral cell membranes (ML) are relatively straight and separated from each other by 200 to 300 Å. Glutaraldehyde, 30 000 x.

Fig. 3. A tangential section through several secretory cells of the lachrymal gland of the stenohaline Graetemys. The elaborate Golgi apparatus (G) and rough-surfaced endoplasmic reticulum (RER), the relatively few mitochondria (M), the numerous secretory droplets (S), and the tightly apposed, straight intercellular borders (arrow) indicate the gland is primarily involved in the secretion of organic material. There is some osmotic damage to this tissue, especially in the mitochondria (M). The stenohaline lachrymal gland was very susceptible to this type of damage, whereas the lachrymal gland from Malaclemys tolerated a wide range of fixative toxicities. Uranyl acetate and lead citrate staining, 30 000 x. Fig. 4. Lachrymal gland from Malaclemys terrapin, kept in 100% seawater. The relatively smooth apical border is bounded by lateral membranes held together by junctional complexes (JC). Basal to these complexes the surface area of the lateral cell membranes is increased by numerous interdigitating microvilli (MV). Glutaraldehyde – osmium tetroxide fixation, Lead citrate staining, 42 000 x.

Fig. 5. A lower magnification view of the cells seen in Fig. 4. The relatively wide lumen is evident. A few secretory droplets (S) are located apically. Glycogen (G) and mitochondria are also prominent features. Desmosomes between interdigitating microvilli on the lateral cell membranes are rare. Lead citrate staining, 20 000 x.

Fig. 6. Lachrymal gland of Malaclemys terrapin, kept in fresh water, showing tenuous basal attachment of the tubular cells through a series of thin projections (arrow). Two basal cells (B) are situated on the basement membrane, between the larger principal parenchymal cells. These contain considerable rough-surfaced endoplasmic reticulum (RER), a few mitochondria (M) and lysosomes (L). Uranyl acetate – lead citrate staining, 15 000 x.

Fig. 7. Lachrymal gland of Malaclemys terrapin, kept in 100% seawater, showing elaborate Golgi apparatus in cross section. Three large vesicles (V) or condensing vacuoles are located between the stacked cisternae. These vacuoles contain a moderately dense material. A lysosome (L), mitochondria (M), and glycogen (G) are present. Uranyl acetate – lead citrate staining, 70 000 x.

Fig. 8. Lachrymal gland showing high power view of a basal cell, and its most prominent features, rough-surfaced endoplasmic reticulum (RER), free ribosomal arrays (arrow), mitochondria (M), and Golgi apparatus (G). The lateral cell membranes in these small cells are smooth. Uranyl acetate staining, 90 000 x.

Fig. 9. Lachrymal gland of Malaclemys indicating the major features of the stroma. A prominent basement membrane (BM) underlies the tubular epithelium (E). Because of spaces between the epithelial projections (arrows), the intercellular space is separated from the subepithelial connective tissue by only the basement membrane. A large patent capillary (C) without nerve endings is located to the top right of the figure. The large central cell is a pigment cell, with rough-surfaced endoplasmic reticulum (RER) and Golgi apparatus (G). The pigment granules (PG) are located against the nuclear membrane. Uranyl acetate staining, 23 000 x.

Fig. 10. The lachrymal gland of Malaclemys showing a nerve ending (N) between two tubular epithelial cells. The nerve ending contains large and small granular vesicles and very short lengths of neurotubular material. The nerve ending is separated from the epithelial cells by a narrow interspace (arrows). Permanganate post-fixation, 66 000 x.

Note: Figs. 1–10 follow.